Visual cortex: **A cat's-eye view of the visual system**

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Optical imaging data show that the cat's visual cortex contains patches of cells that respond to low spatial and high temporal frequencies; outside the patches, cells respond to high spatial and low temporal frequencies. The results suggest a possible anatomical substrate for psychophysically defined spatial frequency channels.

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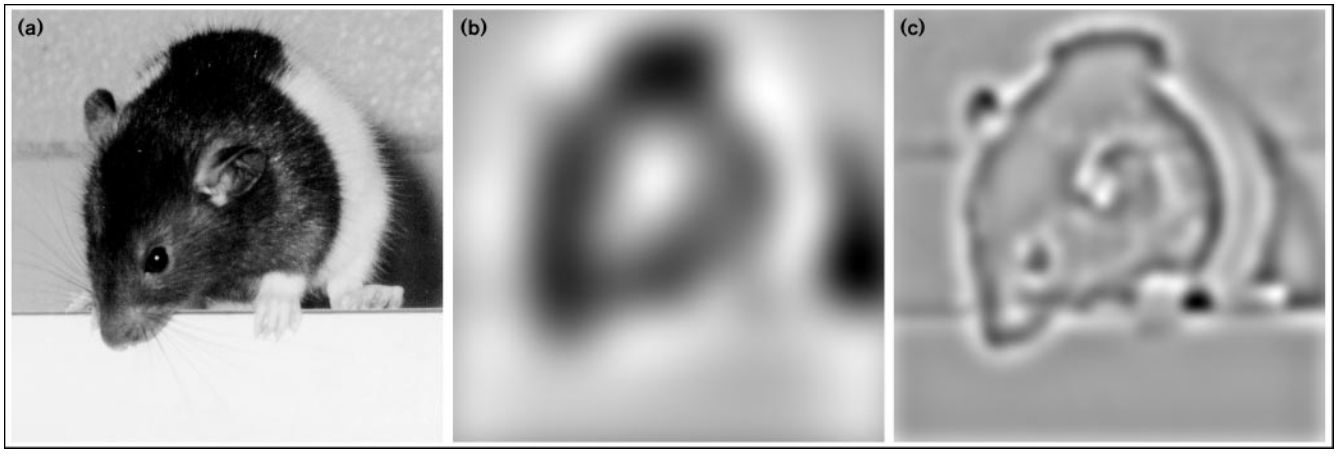
In 1857, Helmholtz suggested that the brain processes sounds by performing something like a Fourier analysis of the sound waveform — breaking it down into its individual frequency components and determining their amplitudes — and there is much evidence to suggest that he was basically correct. Individual fibres in the auditory nerve fire at rates which are mainly dependent on the amplitudes of particular temporal frequency components in the sound stimulus, and because of this, the processing of sound by the brain can be most simply described by reference to the Fourier amplitude spectrum of the sound, rather than to its phase spectrum or the shape of the waveform itself.

Nearly 30 years ago, Fergus Campbell and John Robson [1] made the analogous suggestion that the initial stages of visual processing might require the decomposition of the retinal image into its component spatial frequencies, by neural channels selective for different frequency ranges (Fig. 1). Although it is unlikely that the visual cortex performs anything like a real Fourier transform of the visual world — which would require that the receptive fields of individual neurons cover the entire visual field, and almost none of them do — it remains possible that something like a local patchwise Fourier, or wavelet, analysis is performed.

Although it was controversial, this idea became enormously popular among visual psychophysicists, and it led, amongst other things, to a determined search by (some) neurophysiologists for the neural substrates of spatial frequency channels in the brain. The merits of spatial frequency processing by the visual system have been debated back and forth [2], but no-one questions that the responses of visual cortical neurons are usually selective for the spatial frequency of a sinusoidal grating patch, as well as for its position and orientation. Nor is it questioned that, at any given eccentricity in the visual field, there are cortical receptive fields with a range of preferred orientations and spatial frequencies [3], as predicted by the patchwise-Fourier analysis idea.

Numerous studies have shown that receptive-field attributes such as eye preference, preferred orientation and direction of motion are mapped in an orderly fashion across the surface of the brain. It is natural to ask

Figure 1



Images can be filtered to leave only those spatial frequencies which lie within a certain range (or bandwidth). The image shown in **(a)** has been filtered with **(b)** a low and **(c)** a higher band-pass spatial frequency filter approximately to simulate the information available to neurons within the (b) low and (c) high spatial frequency patches of cat visual cortex. I have assumed that the cat is staring at the rat from a distance of about one or two feet.

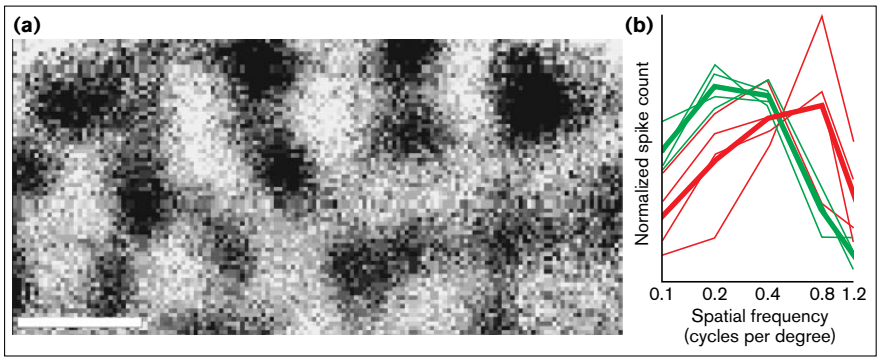
therefore, whether spatial-frequency preference also varies systematically across the brain surface, and a number of studies — which used the 2-deoxyglucose (2-DG) technique for labelling active neurons — have provided evidence, in both cats and monkeys, for sets of columns preferring different spatial frequencies [4,5]. Further interpretation of the results of these studies was difficult, because the 2-DG method requires that the animal be sacrificed after presentation of only one stimulus. The newer technique of optical imaging allows responses of the cortex to many different stimuli to be measured sequentially *in vivo*. An important control that is often performed is to compare the optical responses in specific locations with the responses of single, or small groups of cells, measured with extracellular recording electrodes.

This technique has now been used by Shoham *et al.* [6] to study the organization of spatial-frequency preferences in cat visual cortex (area 17). The results (Fig. 2) confirm the earlier 2-DG findings that spatial frequency has a columnar representation in the cortex. Somewhat surprisingly, though, the experiments show that spatial frequency preference does not vary smoothly and continuously across the cortical surface (as, for example, orientation preference does). Instead, it seems that there are two discrete spatial frequency domains, one containing neurons preferring, on average, a range of low spatial and high temporal frequencies, and the other containing neurons which, on average, prefer a range of spatial frequencies about four times (two octaves) higher, and with correspondingly lower temporal frequencies. The domains are arranged in the by now familiar periodic blob-like pattern (Fig. 2), with the blobs themselves containing the low spatial–high temporal frequency preferring neurons, and the more extensive regions around the blobs containing the high spatial–low temporal frequency preferring neurons.

Functionally and/or anatomically defined blobs of various kinds seem to be ubiquitous in the visual cortices of different mammalian species. Several years ago it was found that there is a blob-like pattern of variation in the amounts of the enzyme cytochrome oxidase in the cat visual cortex [7]. In the macaque monkey and human visual cortex, the distribution of this enzyme is strikingly punctate and regular, and each cytochrome oxidase blob is precisely aligned with the centre of a stripe of cells dominated by input from either the left or the right eye. This degree of geometrical regularity has led many to believe that the cytochrome oxidase blobs in the macaque monkey mark the centres of discrete modular cortical processing units. One might expect that a similar relationship between cytochrome oxidase blobs and ocular dominance patches would be found in the cat, but this appears not to be the case.

Dyck and Cynader [8] used a combination of staining techniques to show that cytochrome oxidase blobs in the cat mark regions which contain relatively lower amounts of serotonin 1C receptors and synaptic zinc: these regions were shown to have no obvious structural relationships with the eye dominance patches revealed in the same tissue sections by trans-neuronal autoradiography. Shoham *et al.* [6] confirmed this result, although further analysis (M. Hübener and D. Shoham, personal communication) has suggested a relatively weak tendency for the centres of the cytochrome oxidase patches to avoid the border regions of the eye dominance patches. Boyd and Matsubara [9] and Hübener *et al.* [10] have shown that the cytochrome oxidase patches in the cat receive inputs selectively from layers of the lateral geniculate nucleus that receive inputs specifically from two of the three different classes of retinal ganglion cells — the so-called Y and W cells. The optical imaging results tie in neatly with this finding, because the Y and W cells are known to be selective for lower spatial and higher temporal frequencies than other retinal ganglion cell classes. It is unlikely however that each Y/W-cell patch receives inputs from only one eye.

Figure 2



Spatial frequency domains in cat area 17. **(a)** In this *in vivo* image of the surface of the cortex, dark regions of tissue have a relative preference for low (0.2 cycles per degree) *versus* high (0.6 cycles per degree) spatial frequency sine wave gratings, whereas lighter regions prefer the higher spatial frequency. (Scale bar = 1 mm). **(b)** Spatial frequency tuning curves obtained from groups of neurons recorded extracellularly from within the low spatial frequency patches (green) and outside them (red). Thin lines are tuning curves averaged over single electrode penetrations; thick green and red lines are the averages over all the penetrations in low and high spatial frequency patches respectively. (Reproduced with permission from [6].)

These new results show that the cat visual cortex contains at least two functionally distinct and semi-overlapping sets of patches: one for spatial frequency, and the other for eye dominance. To this list must be added the iso-orientation domains, and their associated patchy regions of direction preference [11]. It does not seem safe at present to predict whether or not additional sets of patches for other functional properties will be found. Nor is is clear, if there are additional sets, how they might relate structurally to those already known to exist. For the moment however, two conclusions seem reasonable. First, although blobs and patches of various kinds seem to be ubiquitous in mammalian visual cortices, there is no one pattern of organization that is common to all species. Second, the presence of two unrelated and overlapping sets of patches, each with a spacing of about a millimetre, makes it hard to maintain that cat visual cortex is modular on this scale. A module has to have a centre and a boundary, and different sets, and probably numbers, of modules will be obtained depending on whether one chooses the centres of the cytochrome oxidase blobs, or the centres of the ocular dominance patches (or orientation singularities or other feature) for this purpose. This seems unsatisfactory, and it might be more appropriate to characterize cortical organization on this millimetre scale as 'mosaic' rather than 'modular'.

Finally, what of spatial frequency channels? Is visual processing really analogous to auditory processing? The analogy is probably not all that good, but it has certainly been productive. There is now a large body of psychophysical data suggesting that the human visual system contains perhaps two or three temporal frequency channels, and four to six spatial frequency channels with bandwidths of about one to two octaves [12]. To my mind, the estimated number of channels is too small, and their bandwidths too broad, to justify describing early visual processing as a patchwise-Fourier analysis in the spatial (or temporal) domain. But because the number of channels is likely to be small, anatomical correlates of them might not be difficult to identify.

Obvious candidates for these anatomical correlates are the different retinal ganglion cell types projecting to the brain. The cat optical imaging data do not show an unambiguous relationship between retinal cell types and spatial frequency columns though, because at least three retinal cell types — X, Y and W — project to the cortex, and only two types of spatial frequency column have been found. For these reasons, studies of the cortical representation of spatial frequency in the monkey, whose visual system is much more similar to humans than is the cat's, promises to provide valuable information. Optical imaging can be expected to continue to provide materials with which a bridge between visual psychophysics and cellular neuroscience can be constructed.

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